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Cortical representation of motion sequence processing in younger and older adults: an fMRI study

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Processing motion sequences is essential for daily activities such as driving. While aging affects various cognitive and neural functions, how older adults process motion sequences in the brain remains poorly understood. This study investigated age-related differences in the neural processing of motion sequences between younger and older adults using functional magnetic resonance imaging (fMRI). Twenty-four younger and 27 older adults viewed static picture quartets depicting dynamic sports actions and rated the coherence of each sequence on a four-point Likert scale. Stimuli comprised real-life action sequences in three conditions: ordered, randomized, and grid-scrambled. Results demonstrated that while younger adults' ratings consistently tracked stimulus order, older adults showed reduced sensitivity to ordered sequences compared to younger adults, though their ratings remained higher for ordered than randomized sequences. Notably, older adults exhibited enhanced left-lateralized frontal responses, and several clusters showing age differences overlapped with regions commonly associated with the default mode network, including the medial frontal and angular gyri, during randomized sequence processing compared to younger adults. These findings reveal age-related differences in the cortical mechanisms underlying motion sequence processing, with older adults engaging more top-down cortical resources when processing randomized motion sequences. This research provides new insights into how aging shapes the cortical representation of motion sequence information in the brain.

Keywords Aging, fMRI, Apparent motion sequence, Top-down processing, Statistical regularity

The ability to precisely process and anticipate visual motion sequences helps us make better decisions on the street. For example, when driving or walking, accurate processing of the trajectory of moving objects allows people to avoid collisions with vehicles, pedestrians, or even stray animals. Yet, how the processing of motion sequences varies across age remains scarcely discussed[1]. In 2022, the statistics showed that around 8000 older adults were killed by motor vehicle accidents in the United States (2024)[2]. A better understanding of older adults' ability to process motion sequence information thus becomes a crucial issue that can help decrease the casualty[3]. Indeed, older adults had problems with high-speed discrimination during simulated driving, along with compensatory activation in frontal areas and reduced deactivation of the default-mode network[4].

Given the broad neural and cognitive changes associated with aging[5], how does aging affect the processing and prediction of motion sequences? At the behavioral level, older adults perform comparably to younger adults when discriminating light bulb images depicting biological motion patterns such as walking, jogging, and skipping actions[6], but see[7]. However, older adults show reduced discrimination ability than younger adults between forward and reversed rotations in the rectangle orientation task[8]. These discrepancies in age-related effects on biological and implied motion processing may stem from experimental differences in probing concurrent versus projected motion.

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Motion perception consists of registering static images by the retina while our brain spontaneously connects these images and forms a motion sequence representation, a process that may be differentially affected by aging[9]. A more specific understanding of age-related differences in motion sequence processing inferred from static patterns in the brain is needed to address visual processing issues in older adults' daily life activities. For instance, reduced motion sensitivity is correlated with self-reported driving difficulties[10]. As such, understanding how aging affects the processing of motion sequences, both behaviorally and neurologically, can inform car design and road safety measures[11].

Motion sequence processing relies on top-down interpretation of spatial–temporal relations[12], a mechanism that may be particularly relevant in aging due to increased reliance on prior knowledge[13]. Like other forms of inferred motion perception, it requires the visual system to construct a sense of movement that is not physically present in the stimulus stream. This reliance on top-down inference may be particularly pronounced in aging, where perceptual processing is thought to depend more heavily on prior knowledge under conditions of reduced sensory input.

A closely related but different visual process, representational momentum, is the mental extrapolation of complex implied motion from static images[14–16]. Such momentum-like processing reflects a fundamental function in the brain that infers likely states of future events based on current input, particularly for moving object trajectories[17]. Neuroimaging studies further show that processing static stimuli with implied motion engages higher neural responses in the prefrontal cortex, modulated by prior conceptual knowledge about the expected motions of the objects[15,18]. Together, these findings suggest that perceiving motion from static inputs depends on top-down neuropsychological operations that generate implicit expectations of motion, which are, in fact, not physically present. Critically, the same motion-sensitive cortical areas (e.g., the superior temporal sulcus and prefrontal cortex) involved in processing actual visual motion have also been shown to respond to static images that imply motion, confirming that the neural substrates engaged in our task overlap substantially with those identified in the visual motion processing literature.

As visual experience increases with age, it is reasonable to expect more dominant top-down processing in the older adult brain than the younger adult brain during motion sequence processing. Critically, such top-down motion sequence processing in older adults[19,20] may be applied even when the stimuli do not easily afford implied motion. By contrast, motion sequence processing in younger adults should be more sensitive to whether information about implied motion is afforded in the given stimuli, namely, more bottom-up.

Brain imaging studies have shown that aging reduces the distinctiveness of neural responses in perceptual regions, which may alter how visual information is processed[19,20]. With respect to visual motion processing, which shares similar neural substrates with the processing of implicit motion in static images[21,22], Biehl, et al. [23] showed that older adults recruited more activation in the middle and superior temporal gyrus during the processing of low-level radial motion (radially moving circular display of dots) compared to younger adults. By contrast, no significant age differences in brain activation were found during high-level biological motion (point-like walker presenting motion) processing[23]. It is possible that older adults rely more on global information during motion processing that affords compensatory strategies amidst age-related compromises in neural circuits involved in biological motion processing[24]. That is, age-related reductions of perceptual discrimination processing induce older adults to rely more on frontal top-down compensatory operations[19,20,25,26]. In addition, older adult brains should have greater accumulated experience with visual motion stimuli than younger adults[27]. Thus, we hypothesized that older adults could utilize their implicit visual experience during motion processing in a top-down manner by default due to experience.

In this study, we examined motion sequence-related functional neural responses in younger and older adults as they viewed static photograph quartets depicting real-life motion sequences of sports actions and rated the coherence of each sequence in a motion sequence judgment task[28]. Unlike previous studies that used geometric shapes, generic objects[8], or point-light walkers[29], we considered that real-world photographs of human action stimuli are more readily processed by older adults and provide greater ecological validity for assessing their performance. We applied three types of static picture quartet sequences, including Ordered (sequential movements of real-life sports actions), Randomized (shuffled sequences of sports actions), and Control (grid-scrambled pictures from the static images) conditions.

Critically, this is the first study to examine the neural mechanisms underlying age-related differences in motion sequence processing using high ecological validity stimuli (real-life sports action photographs) in combination with both behavioral and fMRI measures. The key innovations of this study are threefold. First, unlike previous studies relying on geometric shapes or point-light walkers, we used naturalistic sports action images, which are more readily processed by older adults and better capture real-world motion sequence demands. Second, we provide fMRI evidence linking age-related differences in motion sequence processing, offering complementary neural indices of top-down processing. Third, we aimed to provide another point of view in aging; rather than interpreting age differences purely as perceptual decline, older adults deploy qualitatively different processing strategies — relying more heavily on internally generated top-down knowledge when confronting ambiguous motion inputs.

Behaviorally, we expected that both younger and older adults would rate the Ordered and Control conditions with the highest and lowest scores, as both groups retain the ability to perceive apparent motion and statistical regularity. In addition, given the top-down knowledge accumulated across the lifespan[13] and its influence on motion sequence processing[30], we predicted that older adults would give higher ratings to the Randomized condition compared with younger adults, reflecting greater top-down influence on motion sequence processing with age.

As for the neuroimaging aspect, both the default-mode network (DMN) and left-lateralization processing can provide indices of top-down cognitive and perceptual processing across age groups. First, the DMN, which includes bilateral medial frontal and parietal areas as well as temporo-parietal junctions, has been linked to top-

down goal-directed executive control processes in the brain[31], and recent work has specifically implicated DMN areas in visual perception through integration of memory-derived knowledge with incoming sensory input[32]. Task-related DMN responses are less suppressed in older compared to younger adults, a pattern interpreted as a reduction in inhibition of irrelevant information[33]. Additionally, DMN activity could also reflect contextual association processing[27], which is crucial for accurate performance on such tasks in older adults[34]. Thus, these findings suggest that the DMN contributes to top-down interpretive influences on perceptual information received from upstream processes[35].

In addition to DMN, hemispheric asymmetries can also index the difference in top-down processing[36]. Greater left-lateralized cortical engagement is typically observed in tasks involving inference and interpretation (e.g., language processing), whereas greater right-lateralized engagement is usually observed in tasks relying more on perceptual processing, e.g., spatial judgments[37,38]. Interestingly, whereas younger adults recruit the right frontal cortex during spatial working memory tasks (i.e., remembering spatial locations), older adults show greater bilateral frontal engagement[39]. Such additional left hemisphere engagement during spatial operations in older than younger adults reflects increased top-down inferential or interpretative operations applied to visual stimuli.

Because motion sequence processing is inherently a top-down process[40], we predicted that older adults would show greater activation in regions overlapping with the DMN and increased left frontal engagement during motion sequence processing relative to younger adults. Such a pattern would be consistent with greater top-down processing of static visual stimuli in older adults, particularly during randomized sequences that contain minimal motion cues. Additionally, we predicted that older adults would show reduced right-hemisphere involvement during the task relative to younger adults, consistent with a shift from bottom-up to top-down processing with age.

Methods

Participants

Sample size requirement was based on a prior related study of age differences in motion processing using rectangular shape stimuli[8], which found greater representational momentum in behavioral judgments in younger than older adults with Cohen's $d = 0.69$. Based on this, G*Power ver. 3 software[41] recommended 23 participants in each age group to reach the power of 0.8 for detecting differences in representation momentum or similar behavioral tasks.

We recruited 24 younger adults (YA) and 28 older adults (OA) Taiwanese adults from Fall 2018 to Fall 2019 in Taiwan, which was more than previous studies investigating similar topics, e.g.,[23,24,42,43]. One older adult was excluded from data analysis due to excessive head movement (>3 mm) during fMRI scanning. Demographic details of the remaining 24 younger and 27 older adults are summarized in Table 1. All participants had Montreal Cognitive Assessment (MoCA)[44] scores equal to or above 26 points, were right-handed, had normal or corrected-to-normal vision (using MR-compatible glasses), and reported no visual impediments, nor neurological disorders and neurovascular problems. The definition of older adults was according to the World Health Organization (WHO), which is 60 years old or above. One of our older adults was 3 months away from his/her birthday to be 60, we thus listed the age to be 59 but considered this participant to be part of the older adult group. Experimenters ensured that participants clearly saw visual stimuli in the experiment through verbal communications with the participants in the scanner. Participants provided signed written informed consent approved by the Research Ethics Committee at National Taiwan University (NTU-REC 201611HS004). The authors confirmed that all methods were performed in accordance with the relevant guidelines and regulations.

Stimuli and procedure

Stimuli were presented using E-prime 2.0 (Psychology Software Toolbox, Sharpsburg, PA, USA) on a desktop computer. Participants viewed the stimuli via a head-mounted display in the MRI scanner with 800 × 600 pixels resolution and 60 Hz refresh rate. For the target display, quartets of the sports-related pictures were presented serially one at a time in grayscale at the center of a black background (Fig. 1). Visual angles of the characters subtended 12° × 16° (height × width) relative to the center of the display.

Experimental stimuli were trials of picture quartets generated based on video clips of sports actions (e.g., shooting a basketball) to make up three experimental condition stimuli. The experimental stimuli were made by our research group, see Supplementary Materials for more details and the pilot rating data. For the Ordered condition, each quartet's four sports action pictures were presented in their preserved temporal sequence order. For the Randomized condition, the sequence order of the same sports action pictures was shuffled within each quartet using E-prime. The Ordered and Randomized stimuli pictures within each quartet were grid-scrambled as the Control condition. There were 72 trials, with 24 trials per condition equally distributed across two fMRI

	Old (N = 27)	Young (N = 24)	Old and Young comparison
Age range	59–82	20–35	–
Age	65.78 (3.07)	22.79 (2.48)	$t(49) = 54.55$, $p < .001$
Gender (Male:Female)	7:20	8:16	$\chi 2 = 0.34$, $p = .562$
Education in year	15.74 (4.18)	16.69 (1.77)	$t(49) = 1.03$, $p = .309$
MoCA	27.96 (1.4)	28.87 (1.33)	$t(49) = 2.38$, $p = .021$

Table 1. Demographic details of the final sample of participants. OA: Older Adults; YA: Younger Adults.

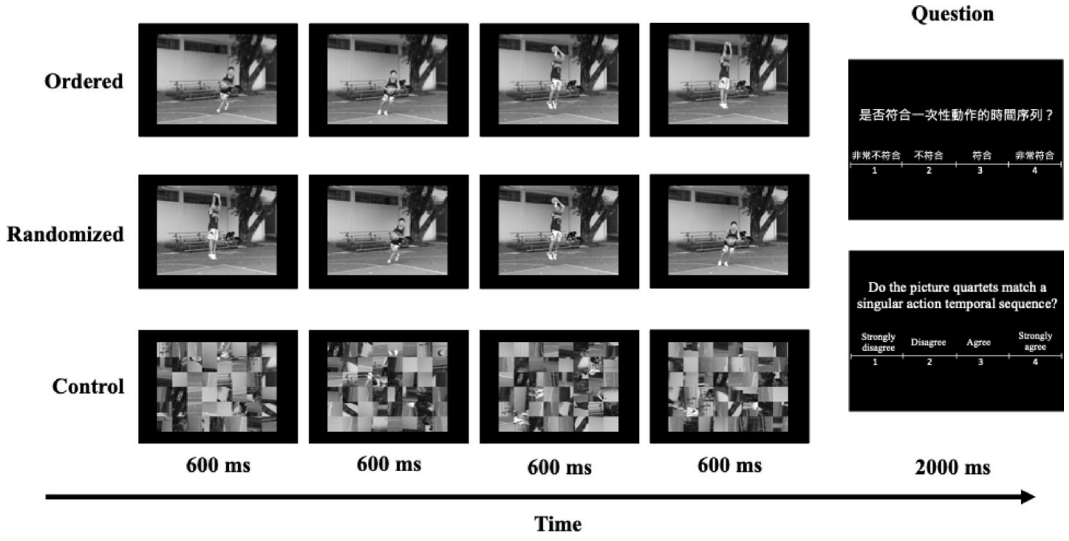

Fig. 1. Sample picture stimuli of the motion sequence judgment task. Picture quartets consisted of real-life picture sequences (Ordered), randomized order of picture sequences (Randomized), or sequences of grid-scrambled pictures (Control). After each quartet, participants saw the Question slide, which asked, "Do the picture quartets match a singular action temporal sequence?" (translated from Chinese). They indicated their judgment on a 4-point Likert scale. The displays are not to scale.

runs, with 12 trials for each condition within a run presented in a random order (i.e., an event-related fMRI design).

Each picture of the quartet was presented sequentially for 600 ms for each trial. After each quartet was completed, the rating question phase followed for 2000 ms, during which participants indicated their judgment rating of whether the picture sequence matches a singular action temporal sequence. Ratings were based on a four-point Likert scale depending on their felt intensity (1 = strongly disagree, 2 = disagree, 3 = agree, 4 = strongly agree) using both hands' index and middle fingers (1 and 2 using the left hand, and 3 and 4 using the right hand). After the question phase, a blank screen was presented with inter-trial intervals (ISI) jittered between 3.6 and 9.6 s before the onset of the next trial.

All participants practiced with 10 trials (different images from the formal task) before the start of the experiment. They were instructed to rate sequences 3 or 4 (depending on their felt intensity) if they considered them to match a single-action temporal sequence, 1 or 2 if they considered them not to match a single-action temporal sequence, and 1 for Control trials (i.e., grid scrambled picture sequence). The rating task allows us to assess how likely the motion sequence matches the representation in each participant's mind, as previous studies used these techniques to evaluate motion fluency (how smoothly and predictably an object moves) between different trajectories[45,46]. Other research also used a similar approach to rate the smoothness of a motion task, see[47–49] for similar usages.

Behavioral data analysis

Mixed two-way analysis of variance (ANOVA) along with effect size (η_p^2) was computed in R[50] and used to assess statistical significance. η_p^2 was provided for all F tests, where $\eta_p^2 = 0.01$ indicates a small effect, $\eta_p^2 = 0.06$ indicates a medium effect, and $\eta_p^2 = 0.14$ indicates a large effect. Cohen's d was computed for each post-hoc t-test, where $d = 0.2$ indicates a small effect, $d = 0.5$ indicates a medium effect, and $d = 0.8$ indicates a large effect[51].

fMRI data acquisition and preprocessing

Scanning was conducted on a 3 T Magnetom Prisma scanner (Siemens, Erlangen, Germany) with a 20-channel head coil at the National Taiwan University Imaging Center for Integrated Body, Mind, and Culture Research. For each participant, two functional runs were acquired using a gradient echo-planar imaging sequence with TR 1000 ms, TE 13.8 ms, flip angle 52°, field of view 220 × 220 mm, voxel size 3.43 × 3.43 × 4.00 mm, 33 axial slices, and 396 scans per run. Axial slices were aligned parallel to the anterior–posterior commissural axis and placed for whole-brain coverage. T2-weighted images coplanar to the functional images were also obtained with TR 7410 ms, TE 103 ms, flip angle 150°, field of view 192 × 192 mm, voxel size 0.66 × 0.50 × 4.00 mm^3, and 33 axial slices for registration. A T1-weighted magnetization prepared rapid gradient echo (MPRAGE) sequence with TR 2000 ms, TE 2.28 ms, flip angle 8°, field of view 256 × 256 mm, voxel size 1.00 mm isotropic, and 192 sagittal slices was acquired for spatial normalization to the Montreal Neurological Institute (MNI) standardized space. The cerebellum part was not included in the scanning protocol.

Brain image data preprocessing and statistical analyses were performed using SPM12 (Wellcome Department of Imaging Neuroscience, London, UK). For each participant, motion and slice timing corrections were first applied to functional volumes. T2 images were co-registered to the functional images, and T1 images were then co-registered to the already registered T2 images. T1 images were spatially normalized using the Diffeomorphic

Anatomical Registration Through Exponentiated Linear Algebra (DARTEL) procedure[52]. The resulting spatial normalization parameters were applied to the functional images, which were re-sampled to 3 × 3 × 3 mm voxel sizes and smoothed with a 6 mm 3D Gaussian kernel.

fMRI data analysis

For each participant, first-level analysis of whole-brain functional data estimated voxel-wise neural responses associated with each quartet condition. A general linear model (GLM) was applied to the preprocessed functional images that included three delta regressors convolved with the canonical hemodynamic response function (HRF) that coded the onsets of the Ordered, Randomized, and Control quartets. Six movement parameters were included as head-motion covariates. Regressors were replicated across the two functional runs, including the run constants. Three contrasts were performed to yield estimates of Ordered – Control, Randomized – Control, and Ordered – Randomized whole-brain neural responses for each individual.

Second-level whole-brain analyses identified brain areas showing age differences in functional neural responses when processing motion sequences during the Ordered and Randomized quartets (relative to the Control) and their differences. Thus, first-level individual whole-brain contrasts were fed into independent samples *t*-tests of younger and older age group differences separately for each of the three contrasts. We further examined brain areas showing motion sequence-related neural response correlations with behavioral ratings across age groups. This involved whole-brain regression analyses for each of the three whole-brain contrasts with individual mean sequence ratings for the corresponding conditions, age, and the interaction between age and ratings, as independent variables. The statistical significance criterion for all group-level whole-brain analyses was a primary uncorrected voxel p-value of < 0.001 in conjunction with a cluster size of 13 contiguous suprathreshold voxels, which fulfilled a whole-brain cluster-level family-wise error rate (FWE) of $p < 0.05$ using AlphaSim with 1000 iterations[53], as how previous studies adjusted for multiple comparisons in aging fMRI studies, e.g., [54–59].

In accordance with its dominant involvement in top-down processing[60], we examined age differences in frontal hemispheric functional lateralization considering the involvement of voxels in contrast responses within a mask of the entire frontal cortex except for the sagittal Sect. 5 mm to the left and right of the midline. For each of the contrasts (Ordered – Control, Randomized – Control, and Ordered – Randomized), Lateralization Indices (LIs) were calculated for each participant's *t*-contrast image data. Specifically, a bootstrap algorithm[61] was applied using the following equation:

$$LI = \frac{Q_{LH} - Q_{RH}}{Q_{LH} + Q_{RH}}$$

where Q_{LH} indicates the integrated contrast t-values of frontal left hemisphere voxels and Q_{RH} indicates the homologue in the right hemisphere. LI ranges from 1 to −1, with positive and negative values indicating left-to-right lateralization. LIs were estimated over sub-sampling iterations, then yielded the mean bootstrapped LI for each condition for each participant.

Functional regions-of-interest (ROIs) were defined using MarsBar[62] as voxels within a 10-mm radius sphere around peak voxel locations in the whole-brain response contrasts across age groups. We conducted correlation analyses between activation levels in regions showing significant age-group differences in the [Ordered – Randomized] contrast and the corresponding differences in behavioral ratings. We focused on this activation contrast but not other contrasts for ROI analysis, as it reflects differences in processing motion sequences with and without consecutive implied motion information. Thus, neural response estimates for the [Ordered – Randomized] contrast were extracted from ROIs for each participant and used in subsequent correlation analyses to validate neural and behavioral associative trends. The correlation analyses went through False Discovery Rate (FDR) correction for multiple comparisons.

Results

Behavioral ratings (Fig. 2A) were analyzed using a two-way ANOVA with Sequence (Ordered, Randomized, Control) as a within-participants factor and Age (OA, YA) as a between-participants factor. Before implementing the mixed ANOVA, we made sure that our data followed the normality assumption of ANOVA by checking the theoretical and sample residual QQ-plot, as shown in Supplementary Fig. 1.

We found significant main effects of Age, $F(1, 49) = 10.8$, $p = 0.002$, $\eta_p^2 = 0.180$, and Sequence, $F(2, 98) = 425$, $p < 0.001$, $\eta_p^2 = 0.897$, as well as a significant Age × Sequence interaction, $F(2, 98) = 45.4$, $p < 0.001$, $\eta_p^2 = 0.481$. Post-hoc analyses qualified that older adult ratings were lower in the Ordered condition [$t(49) = -5.15$, $p < 0.001$, $d = 1.47$], and higher in the Randomized [$t(49) = 6.77$, $p < 0.001$, $d = 1.92$] and Control [$t(49) = 2.92$, $p = 0.016$, $d = 0.840$] conditions than younger adult ratings. Both age groups showed higher ratings for Ordered than Randomized sequences [OA: $t(26) = 5.56$, $p < 0.001$, $d = 1.45$, YA: $t(23) = 19.\ 52$, $p < 0.001$, $d = 6.71$], suggesting that both age groups differentiated Ordered from Randomized sequences. Both age groups showed higher ratings for Ordered than Control sequences [OA: $t(26) = 14.7$, $p < 0.001$, $d = 4.38$, YA: $t(23) = 44.5$, $p < 0.001$, $d = 15.3$] and Randomized than Control sequences [OA: $t(26) = 10.3$, $p < 0.001$, $d = 2.34$, YA: $t(23) = 4.98$, $p < 0.001$, $d = 1.37$].

We further compared the reaction time (RT) data (Fig. 2B) using a two-way ANOVA with Sequence (Ordered, Randomized, Control) as a within-participants factor and Age (OA, YA) as a between-participants factor. We also made sure that our data followed the normality assumption of ANOVA by checking the theoretical and sample residual QQ-plot, as shown in Supplementary Fig. 2. We found significantly longer RT in older adults than younger adults, $F(1, 49) = 13.12$, $p < 0.001$, $\eta_p^2 = 0.21$, and a main effect of Sequence, $F(2, 98) = 32.48$, $p < 0.001$, $\eta_p^2 = 0.4$, but no interaction, $F(2, 98) = 0.33$, $p = 0.719$, $\eta_p^2 = 0.007$. Post-hoc paired t-test qualified that the Control condition had a faster RT than the Ordered condition, $t(50) = 5.66$, $p < 0.001$, d = 0.79, and the Ordered condition

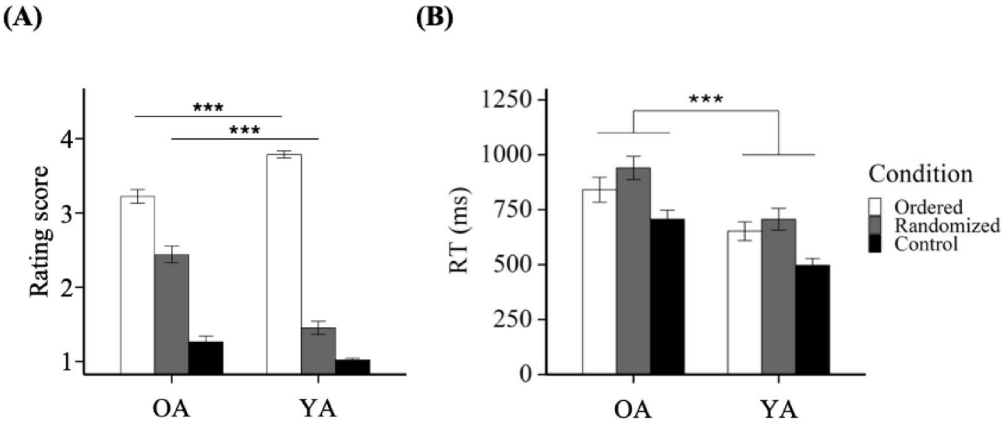

Fig. 2. (**A**) Rating score and (**B**) RT across Ordered, Randomized, and Control conditions for Older Adults (OA) and Younger Adults (YA). Error bars represent one SEM. *** $p < .001$.

had a faster RT than the Randomized condition, $t(50) = 2.97$, $p = 0.005$, $d = 0.42$. The lack of two-way interaction indicated that older and younger adults did not differ in the speed of making decisions across conditions, despite a general slowing effect in older adults[63].

Whole brain responses for Ordered and Randomized relative to Control contrasts separated for younger and older adults are shown in Supplementary Fig. 3, Supplementary Tables 1 and 2. Neural responses were greater in older than younger adults, generally in left hemispheric regions for Ordered and particularly Randomized conditions relative to Control (Figs. 3A and B, Table 2). These brain areas included the left superior, middle, and orbital frontal, angular, and middle occipital gyri, and inferior parietal lobule. Only the medial frontal and precentral areas (for Ordered compared to Randomized conditions; Fig. 3C) in the right hemisphere showed greater responses in older than younger adults. Note that the medial frontal and angular gyrus are part of the DMN.

Neural responses were greater in younger than older adults, generally in right hemispheric regions for Ordered and Randomized conditions relative to Control. These brain areas included the right inferior frontal, calcarine, postcentral gyri, and inferior parietal lobule (Figs. 3D and E, Table 2). Interestingly, the right medial frontal area, which showed higher Randomized than Control condition responses in older than younger adults, showed higher Ordered than Randomized condition responses in younger than older adults instead. Only the left calcarine (for Randomized vs. Control) and precentral (for Ordered vs. Randomized) gyri evinced greater neural responses in younger than older adults (Fig. 3F).

Table 3 shows the results of the LI analyses. LI analyses of the frontal lobes revealed a stronger left-lateralized response in the Randomized relative to Control condition contrast in older compared to younger adults ($t(49) = 9.18$, $p < 0.001$). No age differences in lateralization were found in other conditions ($ps > 0.1$). Thus, older adults, compared to younger adults, engaged a greater extent of neural activity in the left frontal cortex when processing Randomized relative to Control sequences.

ROIs were defined for the bilateral precentral gyri and right medial frontal gyrus (based on Table 2, Ordered relative to Randomized contrast; see Methods). Regression analyses revealed significant interaction effects of ROI response contrasts and age in the left precentral gyrus ($t = 2.32$, $p = 0.025$) and right medial frontal cortex ($t = 2.04$, $p = 0.047$). Pearson's correlations revealed a positive correlation between the rating difference and the activity in the left precentral gyrus in older ($r = 0.649$, $p(FDR) < 0.001$) but not younger ($r = -0.026$, $p(FDR) = 0.905$) adults (Fig. 4). There was a significant difference between the Fisher-Z transformed correlation coefficients between age groups ($p = 0.007$, two-tailed). There were no other significant correlations.

Discussion

Our brain actively predicts the next state of events given its experiences and current sensations[35,64]. In light of this notion, motion-sequence processing in static pictures that imply (but do not contain) visual motion evinces this top-down nature in the neural process. The current findings reveal an age difference in this process, with older adults giving higher scores in motion sequence coherence ratings than younger adults to static pictures depicting shuffled sequences of sports actions (i.e., the Randomized condition). In addition, older adults showed more activation in the DMN and more left-lateralized frontal involvement in the Randomized condition compared to younger adults. Finally, older individuals with less distinction in sequence ratings between the Ordered and Randomized conditions showed less distinction in left precentral responses between these conditions. This brain-behavior association was absent in younger adults, who showed greater left precentral responses in general to Ordered than Randomized conditions. Taken together, our results suggest a greater contribution of top-down processes in older than younger adults in motion sequence processing.

Our finding that older adult ratings in the Ordered condition were lower than those of younger adults could result from the difference in rating criterion. Could the reduced distinction between Ordered and Randomized ratings in older adults reflect a reduction in bottom-up selectivity of neural perceptual responses to different stimuli[20]? We suggest, however, that it is difficult for an age-related reduction in neural perceptual selectivity

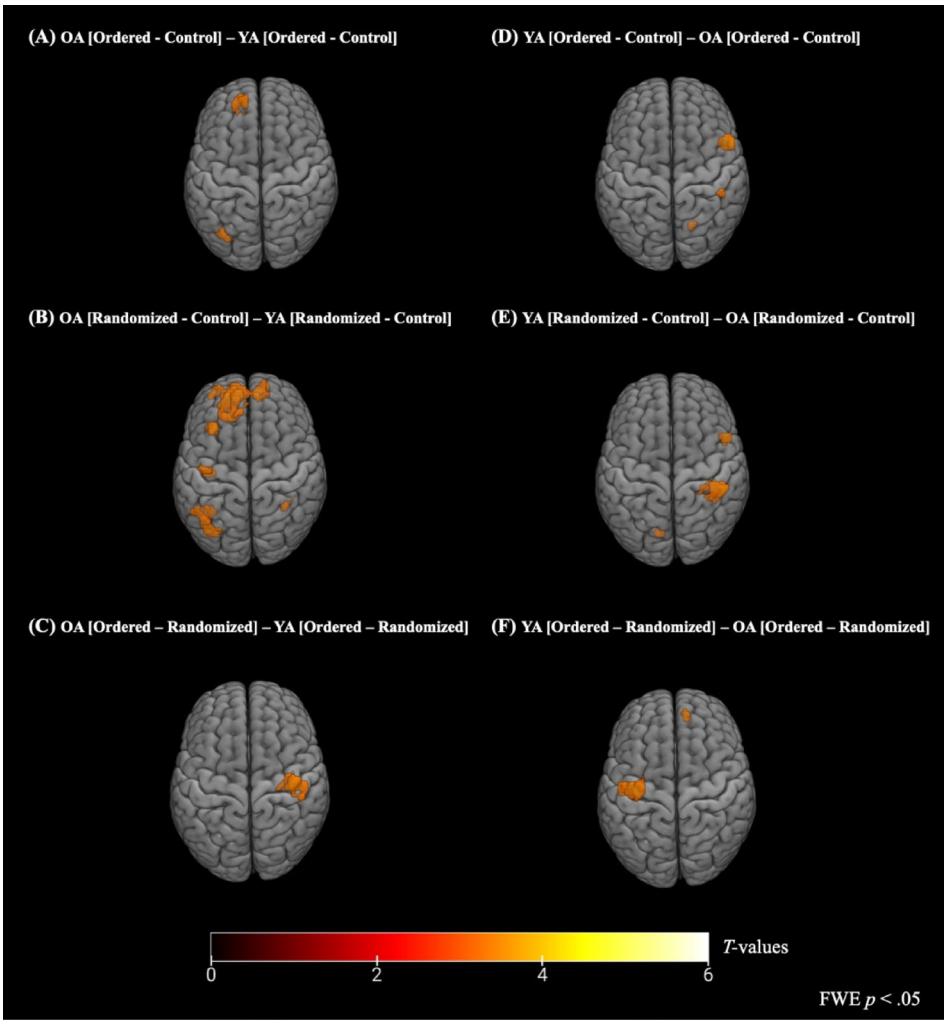

Fig. 3. fMRI statistical activation maps showing age differences in neural responses to the Ordered and Randomized conditions relative to Control and to Ordered relative to Randomized conditions. Brain images are shown in MNI space with statistical overlays thresholded at cluster-wise p(FWE) < .05. OA: Older Adults; YA: Younger Adults.

to account for the joint findings that older adults (a) could differentiate the difference between Ordered and Randomized and between Randomized and Control quartets, (b) engaged greater left frontal responses and more brain regions within DMN, particularly for the Randomized versus Control contrast, and (c) showed individual differences in left precentral (not a perceptual area) responses that correlated with sequence rating differences. Moreover, instructions regarding motion sequence ratings were made explicit and straightforward, with visual differences in the stimuli clearly distinguishable by normative standards. Again, we highlight that the motion sequence judgment task evaluates the perception of apparent motion without real motion features. Thus, we propose that the contribution of bottom-up perceptual processing to age-related differences in motion sequence processing is not primary, at the very least. Instead, lower sequence judgment ratings by older adults in the Ordered condition, given the increased ratings in the Control condition, could reflect an age-related tendency to be more conservative in behavioral ratings for this task[65].

Our rating task captured age differences in motion sequence processing. Our use of sequence ratings to study age effects on motion sequence contrasts with Yes/No judgments used in some previous studies, e.g.,[8]. In the experiments using Yes/No judgments, "No" judgments generally involve greater uncertainty than "Yes" judgments because of the absence of perceptual evidence for a coherent sequence in the former case[66]. The inherent imbalance of the decision criterion in the "Yes" vs. "No" response could lead to a bias in giving more "Yes" than "No" responses. Critically, as older adults could have difficulty assessing uncertainty[67], we thus used a rating task to avoid this problem. Future studies can evaluate age differences in the response ranges adopted in behaviors during visual judgments. Nevertheless, our results clearly demonstrate that older adults retain the ability to differentiate the difference between Ordered and Randomized motion sequences using sequence ratings.

Neural responses to Randomized than Control conditions were more distinctive in older than younger adults in medial frontal and left angular areas, which are parts of the DMN. Chen, et al. [34] previously found

Contrast Name	Region Label	L/R	Cluster Size (Voxels)	MNI Coordinates			T-value
				x	y	z	
OA-YA							
Ordered-Control							
	Superior Frontal Gyrus	L	62	−21	51	27	4.46
	Middle Occipital Gyrus	L	22	−33	−78	39	4.27
Randomized-Control							
	Superior Frontal Gyrus	L	503	−18	54	24	5.88
	Medial Frontal Gyrus	R	–	9	51	24	4.48
	Middle Orbital Gyrus	L	–	−12	51	3	4.44
	Middle Frontal Gyrus	L	43	−33	21	48	4.92
	Angular Gyrus	L	90	−39	−69	39	4.56
	Inferior Parietal Lobule	L	–	−51	−54	48	3.93
	Angular Gyrus	L	46	−36	−54	24	4.48
	Postcentral Gyrus	L	51	−36	−18	48	4.23
	Superior Orbital Gyrus	L	39	−27	57	−3	4.11
Ordered-Randomized							
	Precentral Gyrus	R	182	39	−18	63	5.16
YA-OA							
Ordered-Control							
	Inferior Frontal Gyrus	R	70	54	9	27	5.97
	Calcarine Gyrus	R	15	18	−66	9	4.09
	Postcentral Gyrus	R	14	45	−36	51	3.82
Randomized-Control							
	Postcentral Gyrus	R	149	45	−36	54	5.10
	Inferior Parietal Lobule	R	–	24	−39	51	3.57
	Inferior Frontal Gyrus	R	28	51	12	27	4.51
	Calcarine Gyrus	L	16	−15	−75	9	4.18
Ordered-Randomized							
	Precentral Gyrus	L	181	−36	−18	60	6.15
	Medial Frontal Gyrus	R	21	9	51	24	4.46

Table 2. Peak voxels showing age differences in whole-brain neural response contrasts between Ordered, Randomized, and Control conditions. OA: Older Adults; YA: Younger Adults. Contrasts were thresholded at cluster-wise p(FWE) < .05.

	OA	YA	OA and YA comparison
Ordered-Control	0.43 (0.22)	0.38 (0.3)	$t(49) = 0.67$, $p = .506$
Randomized-Control	0.25 (0.22)	-0.26 (0.16)	$t(49) = 9.18$, $p < .001$
Ordered-Randomized	0.52 (0.21)	0.49 (0.28)	$t(49) = 0.57$, $p = .571$

Table 3. Mean Lateralization Index (LI) and SD (in parenthesis) across conditions in older and younger adults in the frontal lobe. LI: the more positive the value, the more left-lateralized; the more negative the value, the more right-lateralized. OA: Older Adults; YA: Younger Adults.

that DMN processing provides greater support in older than younger adults when accessing retrospective contextual contingencies for current tasks. These findings are consistent with DMN engagement in older adults' information processing that reflects age-related increased access to stored internal, rather than external stimuli, representations during goal-directed task performance[31,32,55]. Alternatively, higher DMN responses in older adults could also indicate reduced inhibitory processing[68] or compensatory activation[4,69,70]. The extra activation in older adults could also suggest the dedifferentiation in neural processing in older than younger adults[71–73]. In our study, however, these possibilities should equally affect brain responses to Ordered, Randomized, and Control conditions. Yet, age-related differences in DMN-related responses to Randomized relative to Control conditions were not observed for Ordered relative to Control conditions, ruling out the inhibitory account.

The DMN functioning can be considered the role of hidden layers in neural networks in reconciling non-linear new regularities and contextual associations[34,74], especially for situations that do not match one's past schema[75]. For Randomized quartets in our task, the positions of visual features in later pictures do not match

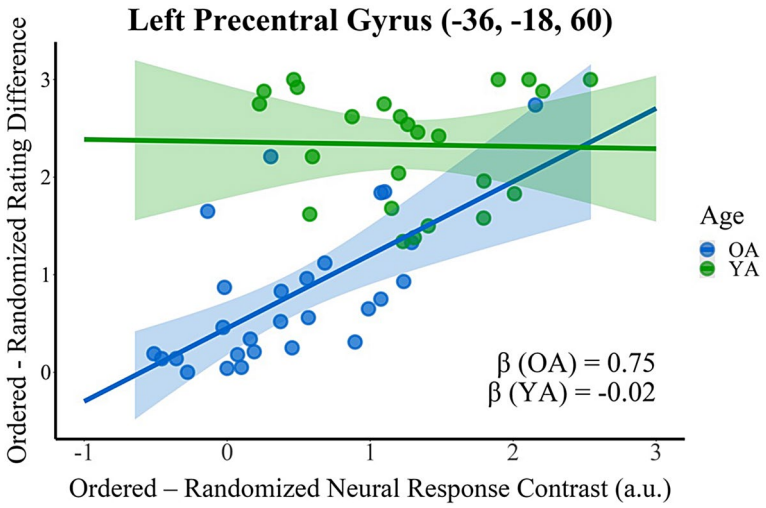

Fig. 4. Scatterplot showing significantly different associations (see main text) between younger and older brain neural response contrasts in the left precentral gyrus on rating score differences for the Ordered relative to Randomized contrast (a.u.: arbitrary units). OA: Older Adults; YA: Younger Adults. The shaded regions represent 95% confidence intervals, and the β values indicate the regression coefficients.

positions predicted from earlier pictures. Thus, non-linear DMN operations may be engaged in older adults to reconcile the discrepancy between predicted and actual pictures. Theoretically, accumulated experiences in older adults should have fortified neural top-down predictive connections for normative stimuli[28,76,77] with visual dynamics associated with smooth motions more frequently in the past. Thus, the older brain could interpret non-normative encounters based on strongly reinforced priors, assigning a low likelihood that the current visual information reflects a randomized motion sequence. Future studies investigating age-related differences in beliefs as a function of life experiences and its influences on decisions are necessary to validate this speculation.

Our finding of right frontal activity in younger adults during motion sequence processing is consistent with a greater reliance on bottom-up processing and increased weighting of sensory evidence. Greater bilateral frontal engagement in older adults compared with more right lateralized activity in younger adults has previously been demonstrated in visuospatial working memory tasks[39] (see[78] for review). We further this by showing that while younger adults engaged the right frontal cortex when making visuospatial motion sequence judgments, older adults showed less right and more left frontal involvement. Studies have implicated right hemisphere processing in more bottom-up, stimulus-driven, modeling of statistical properties of stimulus information[37,38]. By contrast, left hemisphere processing implicates more top-down, model-based, interpretation of sensations[36]. Indeed, for representational momentum studies using visual hemifield manipulations, younger adults' representational momentum effects were stronger for left than right visual field conditions, suggesting that bottom-up processing in the right hemisphere is central for processing representational momentum[79], as a form of motion sequence processing. We propose that greater left frontal involvement during motion sequence processing in older adults, particularly for Randomized quartets, is consistent with a more significant contribution of top-down interpretative processing on sensory information with age. Note that participants were instructed to press 1 or 2 (low scores in rating) when the sequences were not coherent and to press 1 when they saw Control conditions. Despite this, older adults' mean ratings for Randomized and Control conditions were still distinct. Such older adult behavioral responding suggests that top-down processes implicitly "bridged" randomized sequences with internally generated schemas, at least more so than Control sequences.

Older adults with lower [Ordered vs. Randomized] left precentral neural response contrasts (i.e., the left precentral gyrus discriminated less between Ordered and Randomized quartets) showed lower Ordered vs. Randomized rating difference (i.e., Randomized quartets were rated similar as Ordered quartets). This brain-behavior association in individual differences was absent in younger adults, who generally showed clear distinction in behavioral ratings between Ordered and Randomized quartets. The difference in activation in the left precentral gyrus could indicate the differences in motor preparation in the task[80,81]. Another possibility is that predicting ordered sequences could evoke a stronger left precentral activation than random sequences in a statistical regularity task[82]. Thus, the positive brain-behavior association in this region for Ordered vs. Randomized contrast in older adults buttresses the notion that those who extract implied motion even under minimal motion cues do so because they internally perceive greater regularity in the stimuli.

There are several limitations and considerations that should be noted when interpreting the present findings and in guiding future research.

First, individuals may have different levels of knowledge about specific sports. In our study, we did not gather the information regarding how familiar each individual was with specific sports; future studies can consider this to be a participant-level random effect in both the behavioral and fMRI analysis.

Second, we only recruited Taiwanese and right-handed participants in this study; whether the cultural background and handedness homogeneity vary across different populations is beyond the scope of the current

study. A larger sample size will undoubtedly increase the power and robustness of our inference, which can be part of the limitations of the present study.

Third, would the findings here reflect age differences in stimulus–response mapping or task difficulties instead of differences in motion sequence processing? Although our pilot study with younger adults confirmed that the motion sequence was clearly detectable, we did not include older adults in the pilot testing. However, we considered the differences observed are more likely to indicate the difference in top-down knowledge rather than response mapping and differences in difficulties, given that the neuroimaging data showed that older adults were more left-lateralized, whereas younger adults were more right-lateralized when doing the task. Furthermore, the correlation between the behavioral response and the left precentral gyrus in older adults cannot be accounted for by the stimulus–response mapping, otherwise we should have observed similar correlations in younger adults, too. Additionally, if the results were merely reflecting task difficulty differences, we would not have seen the DMN-related brain regions to be more activated in the older than the younger adults; instead, we would have seen the opposite, as the task should be easier for younger than older adults.

Fourth, to ensure that the older adults could complete the task in the fMRI scanner without pressure, we used a relatively small number of trials (24 per condition) in an event-related design. However, statistical efficiency in event-related fMRI depends not only on trial number but also on temporal design (e.g., jittering and randomization), which can substantially improve efficiency even with relatively fewer trials[83], as in our study. The design here thus is sufficient to detect reliable behavioral and neuroimaging differences across age groups.

Finally, while our results indicate that the DMN plays a critical role during rating in older adults, our analyses focused on whole-brain comparisons across age groups rather than network- or seed-based analyses targeting specific DMN nodes. Nevertheless, brain activations within the DMN have been widely used to interpret human behavior across various contexts (e.g.,[34,55,84,85]). Therefore, we believe that our interpretations are well-grounded and provide a meaningful basis for future investigation.

In conclusion, for the first time, we gather both behavioral and neuroimaging evidence and reveal a clear age-related shift in cognitive influences on motion sequence processing. While younger adults exhibit a more bottom-up approach, older adults increasingly rely on top-down processing, particularly in randomized sequences, manifesting as a heightened perception of the apparent motion sequence. Crucially, these age-related differences in motion sequence processing cannot be fully attributed to declines in low-order sensory or perceptual processing, as demonstrated previously in Habak and Faubert[86]. Instead, we propose that this visual processing strategy in older adults reflects the cumulative effect of lifelong experience with normative apparent motion. The unique contribution of this work lies in demonstrating, for the first time using fMRI, that age-related differences in motion sequence processing are accompanied by distinct cortical signatures — specifically, greater DMN engagement and stronger left-lateralized frontal responses in older adults — providing new neural evidence that perceptual changes in aging reflect strategic, experience-driven processing rather than simple sensory decline. Therefore, a comprehensive understanding of visual processing in aging necessitates integrating both the impact of biological changes and the influence of accumulated experiential knowledge over the lifespan.

Data availability

The behavioral data and experimental stimuli are available in the OSF repository at https://osf.io/9mu3r/?view_only=404d2708d3fb4f98a8c07017f76298de.

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Author contributions

S.-L.Y., S.-H.L., J.O.G., L.J., and A.C.T. developed and designed the study. S.-H.L. and Y.-W.K. performed the experiment. S.-H.L., H.-H.L., and Y.-W.K. analyzed the data. S.-H.L., H.-H.L., and S.-L.Y. wrote the manuscript. S.-L.Y. supervised the whole work.

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Declarations

Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Additional information

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